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SEX ATTRACTION IN PAPER WASP, *Polistes exclamans* VIERECK (HYMENOPTERA: VESPIDAE), IN A WIND TUNNEL

H.C. REED and P.J. LANDOLT

Insect Attractants, Behavior, and Basic Biology Research Laboratory Agricultural Research Service, U.S. Department of Agriculture Gainesville, Florida 32604

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Abstract—A wind-tunnel bioassay was developed to test for the presence of sex attractants in the paper wasp, *Polistes exclamans* Viereck (Hymenoptera: Vespidae). Males exhibited significant upwind flight and attraction (chemo-anemotaxis) in response to airflow passed over unmated females, and to hexane extracts of whole bodies and thoraces of unmated females. Unmated females were attracted to hexane extracts of males and to hexane extracts of each body tagma of males, suggesting distribution of the pheromone over the cuticle by grooming. The ectal mandibular and seventh sternal glands are the likely sources of the male-produced sex attractant(s) since extracts of each elicited female attraction in the flight tunnel. These glands are associated with gastral and mandibular rubbing of perch sites by territorial males of *Polistes* species.

Key Words—Insecta, mating, pheromone, attractant, Hymenoptera, Vespidae, *Polistes exclamans*, paper wasp.

INTRODUCTION

The importance of pheromones in mate-finding has been well studied in many insect species, most notably in pestiferous moths. However, the role of sex attractants in the mating biology of social wasps (Vespidae) is not well known. Various researchers have demonstrated experimentally close-range attractants and copulatory stimulants in paper wasps (Post and Jeanne, 1983a, 1984a), polybiines (Keeping et al., 1986), and hornets (Ono and Sasaki, 1987), and others have suggested close-range attractants in yellowjackets (*Vespula*) and hornets (*Vespa*) based on behavioral evidence (Akre, 1982; Batra, 1980; Ross, 1983). Few workers, however (e.g., Ono et al., 1985), have investigated the possibility that vespid pheromones attract mates over long distances. We investigated the role of chemoanemotactic responses to paper wasp pheromones, and thus long-range attraction, in the formation of dispersed mating swarms of sexuals of the paper wasp, *Polistes exclamans* Viereck.

Polistes wasps typically mate away from the nest (Noonan, 1978). In the fall (September–November) males of several temperate species defend and scent-mark perches, presumably for mating purposes (Lin, 1972; Post and Jeanne, 1983b; Turillazzi and Cervo, 1982; Wenzel, 1987) and often form aggregations on hilltops or other prominent landmarks (Beani and Turillazzi, 1988; Mathes-Sears and Alcock, 1986). Males typically press the last few gastral sternites against their perch (Post and Jeanne, 1983b), and some species also rub their mandibles on the substrate (Wenzel, 1987). These behaviors, in conjunction with the presence of large mandibular and sternal glands, strongly suggest that males release pheromone at such sites in order to attract potential mates. Females are known to visit these male perch sites within these aggregations, although infrequently (Mathes-Seares and Alcock, 1986). However, to date, no experimental evidence shows that females are attracted to such marked sites or to male aggregations. In contrast, female paper wasps do not exhibit any obvious calling posture or scent-marking behavior, but Post and Jeanne (1984a) demonstrated that they possess an interspecific, close-range sex pheromone in the venom and a species-specific surface pheromone on the thoracic and gastral cuticle.

We present here demonstrations of attraction in a wind-tunnel bioassay by *Polistes exclamans* males to the airflow passed over unmated females and to extracts of unmated females and, similarly, by unmated females to extracts of males.

METHODS AND MATERIALS

Greenhouse Colonies. Polistes exclamans colonies were collected during late summer and early fall (August–mid-October) in Gainesville, Florida. Adults were vacuumed off nests into Plexiglas traps (Akre et al., 1973), and nest combs were then recovered. Adults were refrigerated until incapable of flight. Males and females were then placed into separate cages (56 × 56 × 57 cm, 28 × 29 × 30 cm, or 21 × 21 × 21 cm) and maintained in different rooms of a greenhouse. Combs were placed in cages and examined daily. Males and females were removed and placed in their respective cages. Individuals from different colonies were placed into separate cages but were mixed after mating trials (see below). Honey and water were placed in each cage. Most caged wasps actively flew between 11 AM and 5 PM (EDT) but aggregated in a corner of their cage the rest of the day. This activity period is similar to the field behavior observed in Florida. Warm temperatures (23–32°C) and bright sunshine (1000–2500 ftc) were required for optimum flight activity. Consequently, wind-tunnel bioassays were done on warm and mostly sunny days during the peak activity periods of the wasps (11 AM to 3 PM).

Females collected on nests should be uninseminated since mating probably occurs away from the nest (Noonan, 1978). In this study, 63 females from collected colonies were dissected and examined for sperm at different times during the fall. Forty-two females sampled from late August to late October were unmated, while five of 21 females sampled in November had sperm in their spermathecae. Thus, larger, fat-laden females from colonies collected from late August through mid-October were likely to be unmated gynes (see Strassman, 1984, for criteria distinguishing workers and gynes) and were selected for use in the subsequent mating trials.

Mating trials were conducted October 10, 13, and 19, 1988, using males and females selected randomly from different colonies to obtain a large pool of females and males showing some sexual activity. One male and one female were placed in a cylindrical plastic container (1 liter) and observed for 5 min. The number of antennations and mounting attempts were recorded for the male, and antennations, escape attempts, and bouts of biting or chasing the male were recorded for the female. Only a few females were successfully mated (four of 324 couplings), because most females were unreceptive to males. A low level of female receptivity was also observed in mating trials with *Polistes fuscatus* (Larch and Gamboa, 1981; Post and Jeanne, 1983c). Approximately half the females (166) elicited two or more mounting attempts by males. These "attractive" unmated females and their "aggressive" male suitors were then randomly used in the wind-tunnel bioassay and as a source of extracts. These male suitors were housed in two large (56 × 56 × 57 cm) cages each containing ca. 80 wasps. The females used were held in two large cages in a room separate from the males.

Wind-Tunnel Bioassay. All bioassays were conducted in a greenhouse in a Plexiglas flight tunnel (0.6 × 0.6 × 2.2 m) positioned 35 cm in front of an exit fan, thereby creating a pulling-type wind tunnel (Baker and Linn, 1984). Seven layers of plastic screen were applied to the upwind end of the tunnel to reduce airspeed to 1 mph (~28 m/min) and create a more laminar airflow. The point source of the volatiles (cotton wick or brass nozzle) was positioned at the upwind end of the tunnel, 16 cm below the top and 10 cm from the upwind end. The plume geometry was determined by releasing titanium tetrachloride at this height (16 cm) from the upwind end and marking the limits of the plume on the sides of the tunnel. This plume height was below the typical flight level of the wasps in the wind tunnel, as they generally flew up against the top or the upper 1/6 of the tunnel. Wasps were released 1.8 m downwind from the source in the center of the plume from a screen cage (7 cm diam., 7.5 cm height). The release platform was a 15-cm-diam. watch glass resting on a ring stand 30 cm below the top of the tunnel. Test insects were placed in the release cages 1–2 hr before the bioassay to minimize handling immediately prior to bioassays. The release cage with a single test insect was gently placed on the watch glass at a slight incline with the opening facing downwind. This allowed the wasp to remain in the plume momentarily before it exited from the cage. Individual test wasps were observed for 2 min and scored for upwind flight, attraction, or chemoanemotaxis (zigzagging upwind flight within the plume; Kennedy, 1983), close-range casting in front of the source (= hovering), and contact with the source. The length of oriented upwind flight from start to closest approach was also noted. Wasps exhibiting attraction were not scored if only observed within 20 cm of the source since this may occur as a visual response (Post and Jeanne, 1984b). The percent responses were analyzed by chi-square test or were transformed (arcsin) and analyzed using ANOVA and Duncan's multiple-range test (Steel and Torrie, 1960). Light intensity, temperature, and relative humidity were recorded during all bioassays. One or two sets of bioassays were usually performed on each day. After each bioassay, tested wasps were returned to one of two large cages each housing ca. 80 wasps of the same sex. The same individuals were not tested on the same day, but were part of a pool of wasps from which selections were made for bioassays on subsequent days. This experimental design and protocol was followed in all subsequent bioassays.

Airflow Chamber Test. This experiment was designed to test the attractiveness of males to pheromones emanating from live females. A system was developed to introduce volatile chemicals from the females directly into the wind tunnel. Twenty unmated females were placed in a glass jar (3.8 liter) positioned on top of the flight tunnel at the upwind end. The jar was blocked from the view of males in the flight tunnel. The jar lid had inlet and outlet nozzles by which air was passed through the jar via a standard aquarium pump. The jar lid was sealed with parafilm to avoid leakage. The air from this chamber was conveyed into the wind tunnel with Tygon tubing and a vertical steel pipe. A brass elbow (i.e., nozzle) on the end of the steel pipe vented the female airstream into the tunnel. Airflow from the nozzle was regulated to 1 liter/hr using a flowmeter (Brooks Sho-Rate 1355). A system control consisted of an empty jar with an identical set up. Ten males were individually tested to the airflow from the empty jar, followed by 10 males flown individually to the airflow from the jar with 20 females. Seven trials of this experiment (N = 70 per sample) were conducted during October 11–18, 1988. The same jar was used for the control throughout the experiment. After each trial the jars and metal tubing and nozzle were washed in water, acetone, and hexane and left in sunlight to air dry. Outlet Tygon tubing was discarded after each trial.

Female Extract Tests. Male flight responses to hexane extracts of whole virgin females and body tagmata were performed in an attempt to isolate the source of a female-produced attractant. Samples of 10 freshly freeze-killed female whole bodies, heads, thoraces, and gasters were each ground with a mortar and pestle in hexane. Each sample was reduced to 2 ml [1 female equivalent (FE)/200 μl] under a N_2 stream and kept in the freezer until tested. The four extract samples were each tested in the same trial at a dose of 1 FE/200 μl hexane in the following sequence: blank (200 μl hexane), head, thorax, gaster, and whole body. Four males were flown to each sample during one trial (20 males per trial), and 10 trials were performed (40 males/sample) during November 3–14, 1988. The extract or solvent was poured onto a brown cotton wick (dyed with Rit cocoa-brown 20 fabric dye) positioned at the upwind end of the tunnel. The wick was mounted on a pin glued to a wire suspended from the tunnel ceiling. The solvent was allowed to dry for 1 min before commencing the bioassay. The wick was removed after each trial and the pin rinsed in hexane and allowed to dry for 5 min while air was flowing through the tunnel.

Male Extract Tests. Responses of virgin females to male extracts were also bioassayed in this wind tunnel in two separate experiments. The first experiment involved females flown to hexane extracts of freshly freeze-killed male whole body, head, thorax, and gaster. These four extracts were prepared in the same manner as in the female extract tests and were tested at a dose of 1 male equivalent (ME)/200 μl. The samples were tested sequentially: blank (200 μl hexane), head, thorax, gaster, and whole body. Four females were flown to each sample during one trial (20 females per trial), and 10 trials were performed (40 females/sample) during November 17–December 3, 1988. The bioassay protocol was the same as described for the female extract tests.

The second experiment was designed to determine more specifically the source of a male-produced attractant. The seventh sternum with its associated gland from 10 freshly freeze-killed males was dissected, placed in 2 ml of hexane, and allowed to soak for 24 hr in a freezer. An aliquot was removed and kept in the freezer until tested. Mandibles and their associated glands from 10 freshly freeze-killed males were dissected in saline and placed in 2 ml of hexane for 24 hr in the freezer. The ectal mandibular gland reservoir was broken with forceps. Extracts were tested at 1 male equivalent (200 μl). These two extracts, a control (200 μl hexane), and a standard (1 head equivalent/200 μl hexane) were tested in the following sequence: blank, sternal gland, mandibular glands, and head. As before, four females were flown to each sample during a trial (16 wasps per trial), and the test was repeated 10 times (40 wasps per sample) during December 6–14, 1988.

RESULTS

Twenty-two of 70 *Polistes exclamans* males exhibited oriented upwind flight within the effluent plume, i.e., chemoanemotaxis, in response to an airstream passed over *P. exclamans* females, but none was attracted to the airflow from an empty jar (Table 1, A). In response to such female volatiles, males also exhibited significantly more upwind flight than in the control trials (Table 1, A). Close-range hovering downwind of the effluent vent occurred infrequently in both cases, and no source contacts were observed. Hovering in front of the nozzle may be a visual response since preliminary trials ($N = 56$, 3 males/trial) revealed no difference in hovering responses of a test (46%) and blank wick (39%) presented simultaneously in the wind tunnel ($\chi^2 = 1.47$, $P = 0.23$). In the field, males and females frequently inspect small objects projecting from a substrate.

Males also exhibited chemoanemotaxis to whole body extracts of unmated females (35%; $N = 40$) significantly more than to hexane alone (3%) (Table 1, B). Each female body tagma also elicited some attraction but only the thorax extract elicited a significantly higher response (25%) than the blank. Although

TABLE 1. PERCENTAGE OF FLIGHT RESPONSES OF MALE WASPS TO (A) AIRFLOW FROM 20 UNMATED FEMALES ($N = 70$ MALES) AND (B) FEMALE EXTRACTS (1 FE/200 μl HEXANE) ($N = 40$ MALES)[a]

Sample	Upwind flight	Chemoanemotaxis	Hover
A. Unmated females			
Empty jar	59a	0a	3a
Female jar	87b	31b	10a
B. Female extracts			
Blank	48a	3a	5a
Head	65ab	18ab	3a
Thorax	70b	25b	10a
Gaster	65ab	15a	3a
Whole body	93c	35b	3a

[a] Values with the same letters in the same column are not significantly different at $P = 0.05$ (A: χ^2 test; B: Duncan's multiple-range test on transformed data).

extracts stimulated more upwind flight than the blank, only the whole body and thorax extract values were statistically greater than the blank values (Table 1, B). As observed in the airflow chamber, test males infrequently hovered in front of the wick (3–10%, Table 1, B) and did not contact the source. Males attracted to the extracts or airflow did not usually fly the entire length of the tunnel ($\overline{X}$ = 68.8 ± 55.6 cm) but often deviated from their forward flight to fly sideways, downwind, or up against the ceiling of the tunnel.

Virgin female wasps exhibited behavior patterns similar to those observed in males, except that the former had a greater tendency to hover and contact the blank or test wick (Table 2). The length of female oriented upwind flight ($\overline{X} \pm$ SD = 98 ± 58.5 cm; N = 116) was significantly greater than that of males ($\overline{X} \pm$ SD = 68.8 ± 55.6 cm; N = 64) (t test, P = 0.001). Attracted females also reoriented to the plume in the 2-min period (42%, N = 101) more than did the males (8%, N = 59) ($\chi^2 = 18.11$, $P = 2.1 \times 10^{-5}$).

Females were significantly attracted to male whole body, head, thorax, and gaster extracts (25–38%; Table 2, A) as compared to the blank wick (0%, Table 2, A). The male head extract elicited the highest attraction response, although not significantly higher than the other body parts, and stimulated significantly more females to hover in front of the source wick (35%) than the blank wick (13%) (Table 2, A). In a subsequent experiment testing specific gland extracts, unmated females exhibited significant attraction to extracts of the sternal gland (38%), mandibular gland (40%), and head (45%). However, there was no sig-

TABLE 2. PERCENTAGE OF FLIGHT RESPONSES OF UNMATED FEMALES (N = 40) TO EXTRACTS OF (A) MALE BODY PARTS AND (B) MALE GLANDS (1 ME/200 μl HEXANE)[a]

Sample	Upwind flight	Chemoanemotaxis	Hover	Contact
A. Male body parts				
Blank	50a	0a	13a	0a
Head	83b	38b	35b	10a
Thorax	75b	33b	28ab	3a
Gaster	73b	25b	18ab	5a
Whole body	90b	35b	28ab	0a
B. Male glands				
Blank	70a	5a	23a	8a
7th sternal gland	88a	38b	28a	0a
Mandibular glands	80a	40b	38a	0a
Head	80a	45b	48a	8a

[a]Values with same letters are not significantly different at P = 0.05 (Duncan's multiple range test on transformed data).

nificant close range response (hover or contact) (Table 2, B). Although each extract stimulated more upwind flight than did the blank, the differences were not significant.

DISCUSSION

Previous research on paper wasp mating biology has documented different potential mating strategies and a diverse array of male behavior. Our results constitute the first experimental evidence of attraction (chemoanemotaxis) of social wasp sexuals to pheromones produced by the opposite sex. Unmated female gynes are attracted to sex pheromones from the mandibular and seventh sternal glands of males (Table 2, B) and produce a sex pheromone that attracts males (Table 1). These attraction responses functioned over a distance of at least 2 m in the flight tunnel. The demonstration of a male-produced sex attractant supports the hypothesis proposed by several researchers that male scent-marking at perch sites attracts unmated females (Landolt and Akre, 1979; Post and Jeanne, 1983b,d; Wenzel, 1987). In addition, we propose that both female and male pheromones play a role in the formation of dispersed swarms of paper wasp sexuals. Such swarms could result from the attraction of female gynes to marking males and the subsequent response of conspecific males to take advantage of optimum signaling locations and upon arrival compete with other signaling males.

As in other species of paper wasps, *P. exclamans* males appear to mark their perches in the field by pressing their gastral sterna against the substrate. In field observations of perching and marking *P. exclamans* males, one male repeatedly marked perches on either side of a nest without brood but laden with females. Others marked perches at cracks and openings in a building that may have been hibernacula entrances. Gaster dragging is a prominent behavior exhibited by perching or patrolling males of several *Polistes* species (Post and Jeanne, 1983b; Turillazzi and Cervo, 1982; Wenzel, 1987), and mandibular rubbing has also been observed in perching *Polistes major* males (Wenzel, 1987); both behaviors are thought to be scent-marking in *Polistes* species. Examined males of *Polistes exclamans* had ectal mandibular glands (genal area = 0.52 mm^2, frons area = 0.50 mm^2) with an outer cell layer surrounding a membranous sac similar to those described for other vespids [Spradbery (1973) for *Vespula*; Landolt and Akre (1979) and Wenzel (1987) for *Polistes*]. Males also had developed (with globose acini; Landolt and Akre, 1979) glands on the seventh abdominal sterna, with no glands evident on sterna 4–6 (Downing et al., 1985). An examination of males of other *Polistes* species (*P. annularis*, *P. dorsalis*, *P. bellicosus*, *P. fuscatus*, *P. metricus*) revealed ectal mandibular glands similar to those in *P. exclamans* (unpublished data). The widespread existence of probable scent-marking behavior and both ectal mandibular and abdominal sternal glands in males of other *Polistes* species support our expectation that male-produced sex attractants occur in other species of *Polistes* as well.

Although male attraction to male-produced pheromone was not investigated in this study, it is possible that such responses occur in nature. Several *P. exclamans* males and a few *P. metricus* males were observed visiting perch sites of marking *P. exclamans* males. This may also account for the large heterospecific aggregations of *Polistes* males and females we have observed at tall buildings, trees, and hills in Florida. However, further research is needed to demonstrate intrasexual and heterospecific attraction to these male-produced pheromones.

The pheromone of the female *P. exclamans* attractive to males appeared to be present on the entire outside of the female wasp, since extracts of each tagma were active in a flight-tunnel bioassay. Highest response rates, however, were obtained with extracts of the thorax (Table 1, B), which contains a pair of prothoracic and mesothoracic glands (Landolt and Akre, 1979) that could be a source of an attractant pheromone. Secretions from this or other exocrine glands, such as the venom reservoir or Dufour's gland, could conceivably be spread over the entire body during grooming. Keeping et al. (1986) and Post and Jeanne (1984a) showed that in other vespid wasps short-range chemical signals are present on the head, thorax, and gaster and also suggested grooming as a possible means of spreading the pheromone over the entire body. Each body tagma of the males elicited female attraction (Table 2), also suggesting distribution of the pheromone by grooming.

The flight-tunnel design and bioassay procedures used in this study should be useful in further research on sexual attraction in other wasp species and will facilitate the isolation and identification of sex pheromones evident here. Information on factors that affect pheromone release or attraction response (e.g., age, time of day, previous exposure, learning, etc.) can now be investigated using this bioassay to clarify the environmental context of this sex pheromone system. Field trials also will be necessary to form conclusions concerning the role of sex attraction in the mating strategies of these wasps.

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